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5.1 Taphonomic Features of Brachiopods

Brachiopods collected from siliceous mudstone facies, including Hushan, Majiashan, Rencunping, Xinmin, Duanshan, Shaiwa, Xiejiaping, Dengcaoba, Dongpan, Paibi and Liuqiao sections, are devoid of abrasional signs. In these sections, they occur sparsely on bedding surfaces and occasionally have articulated valves. These taphonomic features indicate that the brachiopods have been preserved mostly *in situ*,

with little postmortem transportation and reworking.

Brachiopods collected from Huangzhishan, Zhongzhai and Shangname sections also lack abrasional signs, are randomly arranged on bedding surfaces without particular orientation, and many contain articulated valves, all taphonomic features indicating very limited or no postmortem transportation. Brachiopods collected from the Daoduishan section have both complete and incomplete valves, but these valves are randomly arranged on bedding surfaces, suggesting limited transportation. Those incomplete valves possibly have suffered from stirring of storm, an inference also corroborated by the presence of hummocky cross stratification observed in some beds within the Changhsing Formation at Daoduishan (He et al. 2016).

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5.2 Methods of Brachiopod Sampling and Selection of Studied Faunas

The fossil collection began in the summer of 2002 and continued to 2016. As mentioned in the part of Introduction, more than 10,000 brachiopod specimens have been collected from 15 sections in South China. Brachiopods were collected from the Changhsingian or the upper part of Changhsingian and the basal Induan of the studied sections. All brachiopods found during

excavating beds included both complete individuals and fragments. To facilitate quantitative and statistical analyses of brachiopod diversity and body-size changes, we counted brachiopod individuals for each species (including indeterminate species) in each bed. During counting, if both a body fossil and its mold are preserved together, or both the ventral and dorsal valves of the same fossil are preserved, then all of these are counted as one individual. Isolated molds and ventral or dorsal valves found without counterparts, are treated as independent individuals.

In order to investigate the evolution of brachiopod diversity through time, the brachiopod faunas from Huangzhishan, Meishan, Rencunping and Majiashan sections have been chosen for the study. The first two sections represent a shallow-water setting, in contrast to the last two sections which were deposited in relatively deep-water settings. As already outlined in Chap. 4, the ages and correlations of these four sections are well constrained, therefore enabling a detailed temporal analysis of the brachiopod diversity changes. Moreover, the taxonomy of the brachiopods has been studied in detail at the four sections, thus bringing taxonomic consistency and integrity to the diversity analysis.

Alongside the species diversity analysis through time, body-size changes of the brachiopods in varied palaeogeographic settings have also been investigated, using two most commonly found Changhsingian chonetid brachiopod species, *Fusichonetes pygmaea* and *Fusichonetes quadrata*, from five sections (Zhongzhai, Huangzhishan, Daoduishan, Majiashan, Rencunping). These sections have been selected because together they constituted an approximately-defined basinwide bathymetric gradient spanning the shallow-water clastic shelf, shallow-water carbonate platform and ramp, and deep-water siliceous basinal settings. Parallel to this analysis, we also performed a temporal analysis of brachiopod body-size changes to test whether or not, and how, the brachiopod body sizes responded to the end-Permian mass extinction. This analysis was carried out by using two

most commonly found species from three different sections: *Paracrurithyris pygmaea* at Rencunping and Majiashan and *Fusichonetes pygmaea* at Daoduishan. Additionally, the two species were chosen because they both survived the end-Permian mass extinction.

5.3 Definition and Measurement of Body Sizes of Brachiopods

The width of each brachiopod individual refers to the shell width and the length of each individual refers to the shell length (Fig. 5.1). The width and length of all individuals were measured with an electronic calliper to the nearest 0.1 mm. The body size (g) of a brachiopod individual refers to the geometric mean of the length and width, following Jablonski (1996).

The mean size (X) for each species in each bed of the section is determined by the following equation:

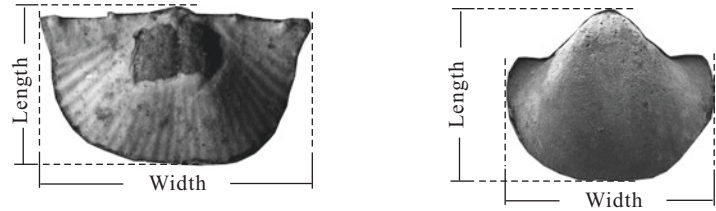
$$X = 1 / N * \sum_{i=1}^N g_i$$

where X equals the mean size, N equals the total number of individuals in a bed of the section, and g is the geometric mean of length and width of each individual in each bed of the section.

The X_{mean} is the average value of geometric means (g) for all individuals of a species through the section. As such, the X_{mean} was used to represent the average size of a fauna in a section.

The X_{median} was also used to represent the average size of a fauna from a section. It refers to the median value of geometric means (g) for all individuals of a species through the section. The X_{median} values from the studied sections were plotted using the software PAST (see Hammer et al. 2001). Usually, the X_{median} is close to the value of X_{mean} and the statistically significant differences of X_{median} from the studied sections can be tested by the Mann–Whitney test (see below). So both X_{median} and X_{mean} are adopted to study the difference of body sizes among different sections (different palaeogeographic settings).

Fig. 5.1 Biometric measurements of varied shell morphology of brachiopods used for this book



5.4 Notes on Other Statistic Techniques

To determine the sampling efficiency to see how well each bed was sampled, a rarefaction analysis was conducted at Huangzhishan, Rencunping and Majiashan (These three sections were sampled for brachiopod collection, proper for the rarefaction analysis; but the Meishan section is a referred section and was not sampled for brachiopod collection in this book, not proper for the rarefaction analysis.) This is an interpolation technique that allows an estimation of how many species would have been found had the sample been larger than it actually was (for the technique see Raup 1975). A curve that is approaching an asymptote indicates that the sample is relatively complete, and any further collection is unlikely to add new taxa, while a curve that is still relatively steep indicates incomplete sampling, as unrecorded species are still likely to be found. The results of rarefaction analysis revealed that most intervals have been well sampled, while the intervals above the mass extinction horizon (or horizons) are less complete, because of the natural scarcity of fossils in these layers (see Fig. 5.2).

To test the numbers of pulses in a mass extinction event before estimating the position of the extinction boundary, the method of Wang and Everson (2007) was used (see Chap. 6). And to estimate the position of a mass extinction boundary for brachiopods near the PTB at the Huangzhishan, Meishan, Rencunping and Majiashan sections and to compare the initial timing of disappearances/extinctions among varied palaeogeographic settings, the improved confidence interval technique of Wang and Marshall (2004) was deployed (see Chap. 6).

5.5 Statistical Tests of the Significance of Body-Size Changes

To investigate the changes of body size at varied palaeogeographic settings and to test whether the body-size changes are statistically significant among the studied sections (Zhongzhai, Huangzhishan, Daoduishan, Majiashan, Rencunping), first, the Shapiro–Wilk test and Histogram (using Software PAST), were adopted to determine whether or not the size frequency distribution in each of the sections followed the normal distribution (Fig. 5.3). For the Shapiro–Wilk test, if the given p is <0.05 , normal distribution can be rejected ($N > 3$ and <5000 , see Hammer and Harper 2006 or <http://folk.uio.no/ohammer/past>) and if $N < 30$, the power of Shapiro–Wilk test is still low (Razari and Wah 2011). Thus, Fig. 5.3a–c and e are not normal distributions ($p < 0.05$). Additionally, both Fig. 5.3h and i are perhaps not normal distributions based on the histograms. Therefore, the results show that most size frequency distributions from the studied sections are not normal distributions (Fig. 5.3). Consequently, the non-parametric Mann–Whitney test (using Software PAST) was used to determine the significant differences in the median sizes (X_{median}) of the brachiopods among the studied sections. The results show that the difference in median sizes between the two groups of sections (i.e., the Huangzhishan and Zhongzhai as one group representing shallow-water settings while the Daoduishan, Majiashan, and Rencunping together representing the other group of moderately deep- to deep-water settings) is statistically significant ($P < 0.05$, see

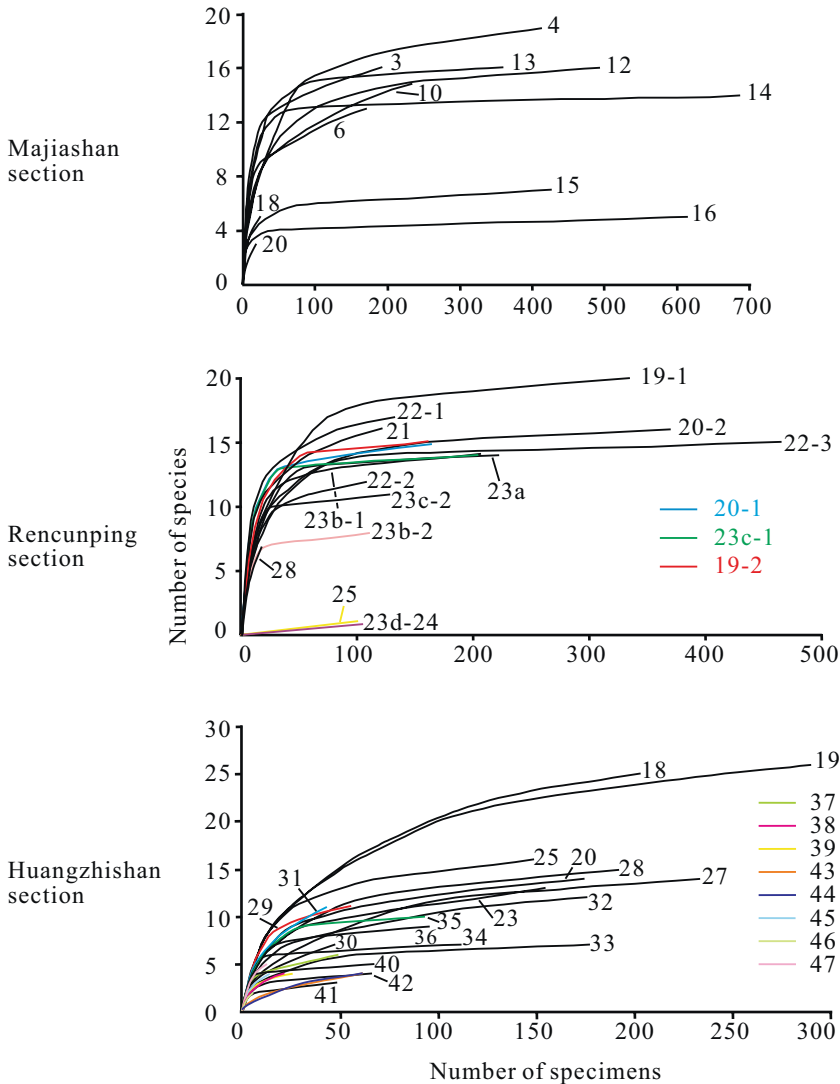


Fig. 5.2 Rarefaction curves (specimens vs. species) for each bed at the studied sections used for comparing the diversity evolution among varied palaeogeographic settings (Revised after He et al. 2015a)

Table 5.1), although the difference of medians for *F. quadrata* is not significant between Zhongzhai and Majiashan ($P = 0.3622$, see Table 5.1).

To investigate whether the brachiopod body sizes before and after the end-Permian mass extinction were statistically different, and to determine whether successively recorded changes in mean body size were statistically significant, we performed the following analyses in steps. First, the mean sizes (the definition sees 5.3 in this chapter) of *Paracurithyris pyg-*

maea from Rencunping and Majiashan and *Fusichonetes pygmaea* from Daoduishan were calculated (details see He et al. 2015a, 2016). Then, the means were subjected to the confidence interval test (He et al. 2015a, 2016). The test has generated the following results: the body sizes of *Paracurithyris pygmaea* significantly decreased from Beds 22-3 to 23a and then significantly increased from Beds 23b to 23d-24 at Rencunping; the body sizes of *Paracurithyris pygmaea* significantly decreased from Beds 10 to 12, followed by a significant

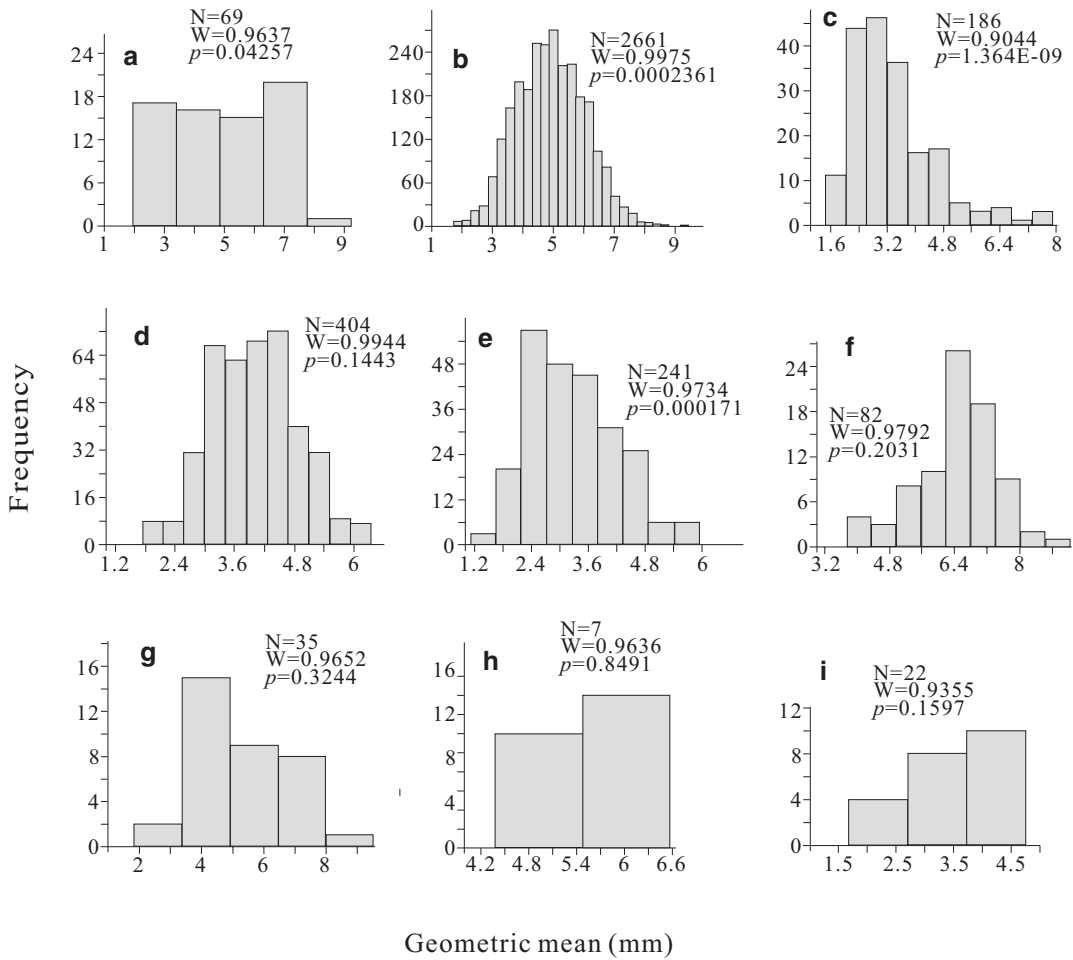


Fig. 5.3 Histograms of size-frequency distribution and results of Shapiro–Wilk test (revised after He et al. 2017). (a–e), for specimens of *Fusichonetes pygmaea*; (f–i), for specimens of *Fusichonetes quadrata*. a, f- Huangzhishan; b, g- Zhongzhai; c- Daoduishan; d, h- Majiashan; e, i- Rencunping. N- number of specimens. W- Shapiro–Wilk test statistic; if the given p is less than 0.05 for Shapiro–

Wilk test, normal distribution can be rejected ($N > 3$ and < 5000 , see Palaeontological Statistics, version 3.0 or <http://folk.uio.no/ohammer/past>) and if $N < 30$, the power of Shapiro–Wilk test is still low, see Razali and Wah 2011), so Fig. 5a–c and e are not normal distributions, and both 5h and i are perhaps not normal distributions based on histograms

increase from Beds 14 to 15 at Majiashan; the body sizes of *Fusichonetes pygmaea* at Daoduishan significantly decreased from Beds 19 to 21 and again from Beds 24e to 26 (Fig. 5.4). These results are strongly corroborated by the outcomes of another two independent tests (Kolmogorov–Smirnov Test and “Jablonski plots”) (see He et al. 2015a, 2016), suggesting the robustness of these derived body-size change patterns.

5.6 Phylogenetic Analysis

The genus *Parapygmochonetes* has some features suggesting affinities with both Subfamily Caenanopliinae Archbold, 1980 and Subfamily Linoproductinae Stehli, 1954. To determine which subfamily the genus should be assigned to, a parsimony analysis was conducted using the software PAUP version 4.0a (Swofford 2002). Parsimony analysis was chosen because among

Table 5.1 *P* values of Mann–Whitney test

| <i>F. pygmaea</i> | | | | | |
|--------------------|--------------|------------------|------------------|------------------|------------------|
| <i>P</i> values | Huangzhishan | Zhongzhai | Daoduishan | Rencunping | Majiashan |
| Huangzhishan | | 0.9531 | 8.962E-11 | 3.92E-12 | 4.085E-05 |
| Zhongzhai | | | 9.48E-55 | 1.448E-78 | 2.381E-53 |
| Daoduishan | | | | 0.7623 | 2.078E-16 |
| Rencunping | | | | | 3.776E-20 |
| Majiashan | | | | | |
| <i>F. quadrata</i> | | | | | |
| <i>P</i> values | Huangzhishan | Zhongzhai | Rencunping | Majiashan | |
| Huangzhishan | | 1.895E-05 | 5.32E-12 | 0.008953 | |
| Zhongzhai | | | 1.251E-05 | 0.3622 | |
| Rencunping | | | | 0.0001465 | |
| Majiashan | | | | | |

After He et al. (2017)

Note: *P* values marked by bold show that the paired populations from two different sections are statistically significantly different with respect to median size at the 95% confidence level ($P < 0.05$)

Fig. 5.4 Variation of means (\bar{X}) of geometric means of the species at Rencunping, Majiashan and Daoduishan (Rencunping and Majiashan after He et al. 2015a; Daoduishan after He et al. 2016). Note: The black area represents the 95% confidence interval of mean; the central line linking the white dots represents the mean at the 95% confidence interval; blue (down) arrows indicate significantly reduced means at the 95% confidence interval; red (up) arrows indicate significantly increased means at the 95% confidence interval

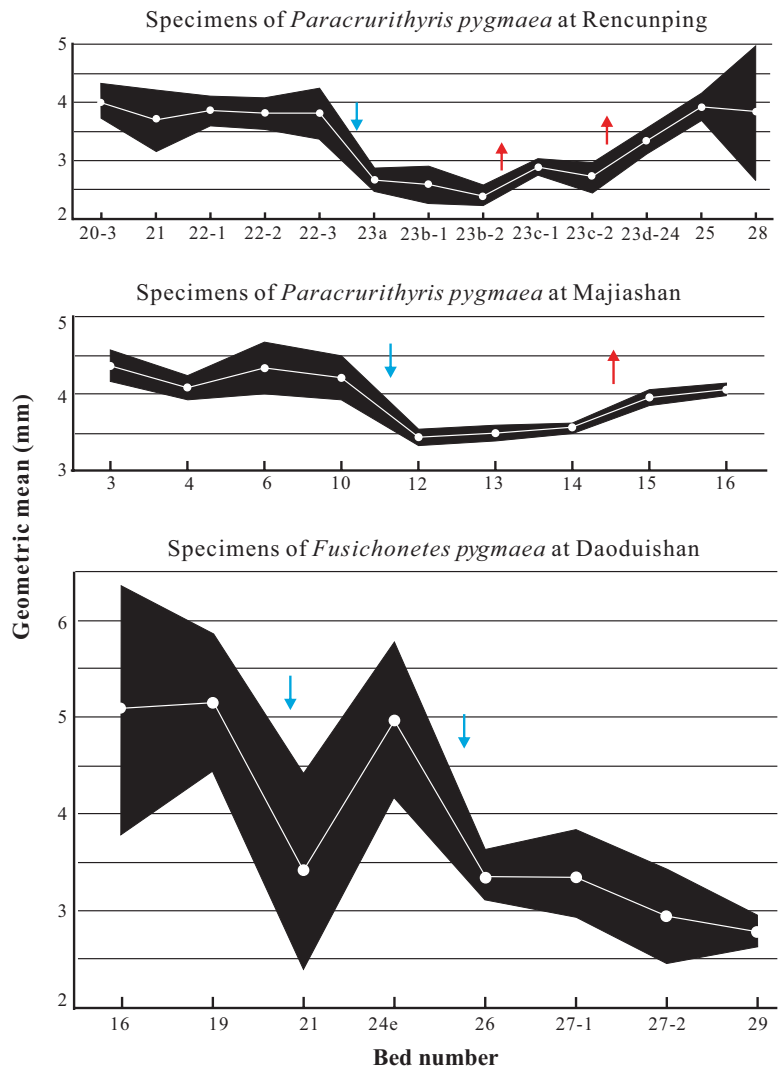


Table 5.2 Character descriptions of the genera of subfamilies Caenanopliinae and Linoproductinae

| NC | Character | Character states (coding) |
|----|---|--|
| 1 | Shell width of type species for each genus | ≥ 1 cm (1), <1 cm (0) |
| 2 | Outline | semicircle/sub-quadrate (0); sub-triangular (1) |
| 3 | Longitudinal profile | strongly- to moderately-arched (0); weakly-arched (1) |
| 4 | Lateral profile | concavoconvex (0); planoconvex (1) |
| 5 | Greatest width | at hinge (0); not at hinge (1) |
| 6 | Flanks | steeply sloping (1); gently sloping (0) |
| 7 | Interarea | Developed (1); not developed or line-shaped (0) |
| 8 | Pseudodeltidium | Developed (1); not developed (0) |
| 9 | Ears | Large (1); small to medium (0) |
| 10 | Ears radially- or concentrically-ornamented | Smooth or radially-ornamented (0); concentrically-ornamented (1) |
| 11 | Ears spinosely-ornamented or not | Spinose (1); no spine (0) |
| 12 | Costellae bifurcated or not | Bifurcated (1); no bifurcation (0) |
| 13 | Costellae strong or weak | Coarse/strong (1); thin/weak/smooth (0) |
| 14 | Costellae wavy or straight | Wavy (0); straight (1) |
| 15 | Ventral spines | Present (1); absent (0) |
| 16 | Dorsal spines/dimples | Present (1); absent (0) |
| 17 | Endospines/papillae | Present (1); absent (0) |
| 18 | Tail | Present (1); absent (0) |
| 19 | Marginal ridges | Present (1); absent (0) |
| 20 | Ventral median septum | Present (1); absent (0) |
| 21 | Dorsal median septum | Present (1); absent (0) |
| 22 | Dorsal accessory septa | Present (1); absent (0) |
| 23 | Interspace between costellae | Wide or weak (0); narrow but prominent(1) |

NC- number code for characters

all approaches of phylogenetic analysis, it is probably the most intuitive (Jaynes 2003; He et al. 2015b) and requires the smallest number of character changes to suggest the most likely correct phylogenetic inference (Sober 1983; Jaynes 2003). The detailed analytical procedure follows Jaynes (2003).

Most of the 24 genera known in the subfamilies of Caenanopliinae Archbold, 1980 and Linoproductinae Stehli 1954 have been selected for the parsimony analysis. *Mistproductus* Yang (1991), *Bandoproductus* Jing and Sun (1981), *Corbicularia* Ljaschenko (1973), *Costachonetes* Waterhouse (1975) and *Costachonetina* Waterhouse (1981) were excluded because of their uncertain generic identity or poor knowl-

edge of interior features. A total of 23 characters were coded for the studied genera (Table 5.2). All characters were equally weighted in the quantitative analysis (Table 5.2). All of these 23 characters occurring in each genus were carefully checked and verified based on the features (details of values see Table 5.2), and then tabulated in the data matrix (Table 5.3). Except for the ingroup taxa that were targeted for the parsimony analysis, two outgroup taxa (*Chlupacina* Havlíček and Racheboeuf 1979 and *Leptoconetes* Havlíček and Racheboeuf 1979) from phylogenetically different groups were included in this analysis (Table 5.3). The result of the phylogenetic trees is given in Chap. 9.

Table 5.3 Characters dataset of ingroup genera within the subfamilies Caenanopliinae of Racheboeuf in Williams et al. (2000) and Linoproductinae of Brunton et al. in Williams et al. (2000) (including the study genus *Parapygmochochetes*) and both outgroup genera *Chlupacina* and *Leptochochetes*

| List of genera | Characters | | | | | | | | | | | | | | | | | | | | | | |
|----------------------------------|------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
| <i>Caenanoplia</i> | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| <i>Arcuaminetes</i> | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | ? | 1 | 1 | 0 |
| <i>Caplinoplia</i> | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| <i>Celtanoplia</i> | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| <i>Devonaria</i> | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 1 | 0 |
| <i>Globosochonetes</i> | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| <i>Klocrinetes</i> | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| <i>Permochonetes</i> | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | ? | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Plicanoplia</i> | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| <i>Semicaplinoplia</i> | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| <i>Songzichonetes</i> | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| <i>Subglobosochonetes</i> | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pygmochetes</i> | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| <i>Parapygmochochetes</i> | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| <i>Linoproductus</i> | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 1 |
| <i>Balakhonia</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | ? | 1 | 0 | 1 |
| <i>Coolkilella</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | ? | 1 | 0 | 1 |
| <i>Fluctuaria</i> | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | ? | ? | 1 |
| <i>Kasetia</i> | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | ? | ? | 0 | 1 |
| <i>Marginovaria</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | ? | 1 | 0 | 1 |
| <i>Chlupacina</i> | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Leptochochetes</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |

“?” = unknown; Number 1, 2, ..., 23 in the second line equal to the NC (the number for each character) in Table 5.2; the feature or its measurement for each character of *Parapygmochochetes*, based on the specimens of this book and those of other genera, based on the figures of Treatise (Williams et al. 2000)

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